Effects of neckbands on survival and fidelity of white-fronted and Canada geese captured as non-breeding adults

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ABSTRACT   *We conducted an experiment to examine the effect of neckbands, controlling for differences in sex, species and year of study (1991-1997), on probabilities of capture, survival, reporting, and fidelity in non-breeding small Canada (*Branta canadensis hutchinsi*) and white-fronted (*Anser albifrons frontalis*) geese. In Canada's central arctic, we systematically double-marked about half of the individuals from each species with neckbands and legbands, and we marked the other half only with legbands. We considered 48 a priori models that included combinations of sex, species, year, and neckband effects on the four population parameters produced by Burnham's (1993) model, using AIC for model selection. The four best approximating models each included a negative effect of neckbands on survival, and effect size varied among years. True survival probability of neckbanded birds annually ranged from 0.006 to 0.23 and 0.039 to 0.22 (Canada and white-fronted geese, respectively) lower than for conspecifics without neckbands. Changes in estimates of survival probability in neckbanded birds appeared to attenuate more recently, particularly in Canada Geese, a result that we suspect was related to lower retention rates of neckbands. We urge extreme caution in use of neckbands for estimation of certain population parameters, and discourage their use for estimation of unbiased survival probability in these two species.*

1 Introduction

The use of alphanumerically coded neckbands is a potentially valuable tool for understanding biology of geese. Neckbands are useful for describing distributions

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of geese throughout the year (e.g. Hestbeck *et al.*, 1991). Additionally, they may be used to estimate survival and population size with capture-recapture models if neckbanded geese are encountered during the annual cycle and some modelling assumptions are met (Hestbeck *et al.* 1990). Usually, survival estimation is the intent of marking geese with neckbands, and has been advocated over solely legbanding to increase the precision of survival probability estimates generated from band recovery models (Brownie *et al.*, 1985, Hestbeck *et al.*, 1990).

However, 'if marking decreases the animal's survival rate, serious negative bias can occur to the survival rate estimators' (Pollock *et al.*, 1990, p.25). Similarly, 'the assumption of no tag loss also is very important ... the result is underestimation of survival rates ... tag loss will cause a decrease in precision of estimators even when it can be estimated and the estimators adjusted' (Pollock *et al.*, 1990, p. 26). Thus, the important assumption is that there is no interaction between either natural or hunting mortality, and the presence of neckbands should be verified if survival probability is estimated using sightings of neckbands.

Use of neckbands has been suspected to cause significant mortality in some species (e.g. Ankney, 1975; Craven, 1979; but see Raveling, 1976). Compared to the number of studies that use neckbands to estimate various population parameters, there have been few studies that have evaluated effects of neckbands on survival and recovery rates of geese (e.g. Samuel *et al.*, 1990a; Castelli & Trost, 1997; Menu *et al.*, 2000; Schmutz & Morse, 2000). In each of these cases, estimates of the potential effects of neckbands on survival probability were not obtained from experimental studies. Although inference from these studies was weak, most of these studies suggested that survival was negatively influenced by neckbands depending on which age or sex cohorts were considered.

The use of neckbands on geese in arctic Canada has increased substantially since 1987 as part of coordinated banding and monitoring networks designed to update annual distribution of Lesser Snow (*Chen caerulescens*) and Ross's geese (*Chen rossii*), and since 1990, of white-fronted and Canada geese. The primary objective of our study was to assess if survival of white-fronted and small Canada geese was affected by plastic neckbands. To our knowledge, this is the first attempt to address this question using geese in an *a priori* experimental design with treatments (neckbands) assigned in a sequential fashion alternating between experimental and control birds.

2 Study area

The Queen Maud Gulf Migratory Bird Sanctuary contains abundant populations of both white-fronted and small Canada geese. Systematic helicopter surveys of the sanctuary during nesting in June 1990 (Alisauskas, 1990), indicated that these birds occur in medium (1-5 geese/km^2) densities along most of the entire coastal portion of the sanctuary and high (> 5 geese/km^2) densities of white-fronted geese between the Perry ($\sim 67°40'$N, $102°10'$W) and Ellice Rivers ($\sim 68°0'$N, $104°0'$W).

3 Field methods

Flightless geese were captured during remigial moult (10 July-10 August, 1991-99) by driving them into portable nets with a Bell 206b helicopter (Timm & Bromley, 1976). Each year, duration of banding ranged 6-12 days except in 1991 (17 days—see below). Flocks of non-breeding birds (composed largely of adult-

plumage geese) were targeted; rarely, small family groups were captured with non-breeding flocks, although such flocks that included young, and presumably their parents, were very common in the study area. We banded all birds with metal legbands. We refer to control geese marked with only legbands as *legbanded* geese. In all years 1991-96, except 1991 and 1992, we systematically selected every other captured goose as an experimental bird and we marked these geese with a neckband and a legband (hereafter *neckbanded* geese). Double-wrap, thin (~ 1 mm thickness) and flexible plastic neckbands were applied to Canada geese: outside diameter ~ 45 mm; inside diameter ~ 40 mm; height ~ 40 mm. Single-wrap thick (~ 2 mm thickness) rigid plastic neckbands were applied to white-fronted geese: outside diameter ~ 45 mm; inside diameter ~ 40 mm; height ~ 50 mm. Neckband design was thus specific to each species of goose to conform with the protocol used for the extensive marking effort of both species across arctic Canada. Both types of neckbands were made of laminated plastic with a three-character alphanumeric code engraved with black codes on yellow neckbands for Canada geese, and white codes on blue neckbands for white-fronted geese. As a goal, we attempted to capture and apply neckbands to 1000 white-fronted geese/year, and as many Canada geese as were captured with them. In 1991, a helicopter crash interrupted field work; up until the crash, a neckband was placed on every other goose, but after the crash, each white-fronted goose received a neckband; neckbands continued to be applied to alternating Canada geese. In 1992, neckbands were placed on alternating Canada geese, but neckbands were placed on the first ~ 1000 white-fronted geese, after which this species had only legbands applied, as stipulated by the funding source for neckbands. In some years, all available white-fronted goose neckbands were used, after which captured white-fronted geese had only legbands applied; in those years, there were more control than experimental geese captured and released. Occasionally, geese banded before 1991 were recaptured. Such recaptures were treated as first captures for this study, and were considered as experimental if they had a neckband, or control if no neckband was present. We also captured 1085 goslings (birds hatched the year of banding), mostly (90.5%) in 1990 and 1991. If a banding drive contained > 4% goslings, we reasoned that the sample contained breeding adults, based on a frequency distribution of % goslings/drive. We wished to standardize methods by targeting non-breeding adult geese, so first encounters from such drives were censored from input data. However, we included individuals marked as goslings in the analysis as first captures when they were captured in subsequent years as adults. We did not place neckbands on geese in 1997-99, but we recorded neckband codes of recaptured birds during continuing operations for banding geese with only legbands. We obtained data on recoveries of marked birds from the Bird Banding Laboratory. We used recoveries of birds shot by hunters between September and March during the winters 1991/92-97/98 for subsequent analysis. We marked 17 453 geese, 1991-97 (Table 1), including 12 344 white-fronted geese and 5109 Canada geese, and obtained 1330 and 697 recaptures (1992-97) of white-fronted and Canada geese, respectively. During the winters 1991-98, hunters shot and reported recoveries of 1012 and 343 white-fronted and Canada geese, respectively.

4 Estimation of population parameters

We estimated all parameters and associated variances using program MARK (White & Burnham, 1999). We estimated true survival and fidelity probability as

TABLE 1. Number of white-fronted and Canada geese marked and recaptured with legbands only, or legbands and neckbands, at the Queen Maud Gulf Bird Sanctuary, NU, 1991-1997. Total number of recaptures and number of individuals recovered (1991-1998) is also reported.

Species	Treatment	Sex	No. marked	No. of recaptured	No. recovered
White-fronted Goose	Legband only	Female	3174	378	210
		Male	3999	397	283
	Legband + neckband	Female	2279	250	231
		Male	2892	305	288
Canada Goose	Legband only	Female	1377	205	78
		Male	1375	185	85
	Legband + Neckband	Female	1219	170	99
		Male	1138	137	81

a non-breeder for our sample of white-fronted and Canada geese using Burnham's (1993) model, which combines band recovery and recapture data. We restricted our analysis to data gathered between summer 1991 and winter 1998, because no geese were neckbanded after 1996 and recovery information was likely incomplete for more recent winters. Survival probability of legbanded (S_t^l) and neckbanded (S_t^n) geese was defined as the probability that a bird alive at the termination of banding in year t survives until the end of banding in year $t + 1$. Fidelity probability of legbanded (F_t^l) and neckbanded (F_t^n) geese was defined as the probability that a bird alive and present in the study area in year $t - 1$ does not permanently emigrate from the study area nor permanently become a breeder within the study area in year t. We considered non-breeding geese and geese that failed at breeding, so a bird could 'permanently emigrate' either (1) through movement to a moulting or breeding area outside our study area or (2) by successfully breeding within our study area for the remainder of the study. Thus, our estimate of fidelity probability includes the probability of remaining a non-breeder on our study area. We also estimated detection (p_t) as the probability that a bird alive and associated with the population of non-breeding geese in year t is captured. For all models, p_{1998} was constrained to equal 1, because this parameter was confounded with year-specific estimates of fidelity probability (White & Burnham, 1999). We used a modified version (see Seber, 1970; Catchpole *et al.*, 1995) of the model described by Burnham (1993) to estimate reporting rate (r_t, also known as conditional detection rate) as the probability that a bird dying during the winter of year t and $t + 1$ is retrieved and reported by the hunter, rather than recovery probability, f, used in most past analysis (Brownie *et al.* 1985). Thus, $r_t = f(1 - S)^{-1}$, and is the parameterization used in program MARK (White & Burnham 1999), to reduce confounding between survival probability and band recovery. We considered four possible sources of variation for each parameter: year, species, sex and neckband.

Our approach to modelling was to test fit of our most general model to the data and then construct a candidate set of models with a reduced number of parameters, based on our biological knowledge of the study system (Burnham & Anderson, 1998). Our global model included all sources of variation (sex, species, year and neckband) and all possible interactions among these effects for each parameter except r. For r, we were interested only in year and marker effects because we had no evidence to suggest that retrieval or reporting probabilities would vary by species or sex. In addition, our structuring of r was motivated by the findings of Menu

et al. (2000). We tested goodness-of-fit of the global model using 100 parametric bootstrap simulations with Program MARK. We computed the probability of observing the deviance for the original data by ranking, in ascending order, the deviance from the original data and those from the simulations. Deviance from the original data was greater than 95% of the simulated deviance, we concluded that the global model did not fit the data adequately. Poor model fit may result from overdispersion (lack of independence and heterogeneity) in the data or poor model structure; further, it may cause negative bias in estimates of variance and inaccuracies in criteria (see below) used to select among competing models (Anderson *et al.* 1994). We therefore estimated a variance inflation factor ($\hat{c}$) to adjust variance estimates and model selection criteria. We estimated $\hat{c} = 1.236$ by dividing the deviance from the global model with original data by the mean of the deviances from the bootstrap simulations described above (White *et al.*, in press), and adjusted estimates of variance and QAIC_c (see below) values accordingly (Burnham & Anderson, 1998).

We selected among competing models using Akaike's Information Criteria (AIC) after adjusting for effects of sample size (AIC_c) and overdispersion (QAIC_c, Anderson *et al.*, 1994; Burnham & Anderson, 1998). QAIC_c values are used to select the best approximating (hereafter, best) model for the data based on the principles of parsimony and trade-offs between under- and over-fitting models (Burnham & Anderson, 1998). The best model was that with the lowest QAIC_c value, and other models were ranked relative to deviations from the best model (ΔQAIC_c). Using program MARK (White & Burnham, 1999), we also calculated QAIC_c weights (w_{QAIC_c}) for each candidate model (Buckland *et al.*, 1997), which represent the weight of evidence in support of each model in the candidate set, given the data. We considered parameter estimates and model structure of all models with $\Delta \text{QAIC}_c < 4.0$ and used w_{QAIC_c} to determine support for such models (Burnham & Anderson, 1998). Variance in differences between parameter estimates, e.g. $\text{var}(\hat{S}_t^l - \hat{S}_t^n)$, was calculated as $\text{var}(\hat{S}_t^l) + \text{var}(\hat{S}_t^n) - 2\,\text{cov}(\hat{S}_t^l, \hat{S}_t^n)$.

5 Estimation of neckband loss

Previous studies have documented loss of neckbands from animals (Hestbeck & Malecki, 1989; Samuel *et al.*, 1990b), which may result in biased estimates of population parameters under some sampling schemes (Nichols & Hines, 1993). We obtained data on rates of neckband loss from geese by recapturing marked birds that were originally marked with both legbands and neckbands. We never observed legband loss from neckbanded geese. Neckband loss did not bias our estimates of population parameters, because each recaptured goose could still be identified by its legband. However, loss of neckbands may bias our estimates of neckband effect on survival (i.e. difference in survival probability of geese marked with legbands and those marked with both legbands and neckbands), because we classified geese as experimental (marked with legbands and neckbands) or control (marked only with legbands) based on the their initial marking. We predicted that if geese lost neckbands, our estimates of marker effects would be biased low because our sample of originally neckbanded geese would include some geese that only retained a legband after losing their neckband.

In previous studies, tag loss was modelled with the assumption of equal survival probability of neckbanded and legbanded birds (e.g. Nichols *et al.*, 1992), because all or most birds in those studies were initially marked with neckbands. Our

experimental study included samples of legbanded and neckbanded geese and we therefore modelled neckband loss using multistate models (Brownie *et al.*, 1993) with two states: (1) neckbanded or (2) legbanded. Geese were initially assigned a state (under our control), but neckbanded geese could assume a legbanded state following neckband loss (beyond our control). With multistate models and program MARK, we estimated k state-specific capture probability (p_t^k) and apparent survival probability (ϕ_t^k), i.e. the probability that a bird alive in year t survives and does not permanently emigrate from the banding site or permanently become a breeder on our study area between year t and year $t+1$ during the course of our study. Therefore, in this analysis, true survival probability (S) and fidelity probability (F) are confounded ($\phi = S \cdot F$). We estimated loss rate (ψ_t^{nl}) as the conditional probability that a goose alive and marked with a neckband (n) in year t loses its neckband (l) between year t and year $t+1$, given the bird survived between years, did not permanently emigrate from our study area, and did not permanently enter the breeding cohort on our study area. Geese that were initially marked with legbands only were not subsequently neckbanded and geese that lost their neckbands were not remarked with these markers if they were recaptured, so ψ^{ln} was constrained to equal 0.

For this analysis we used 1991-1999 banding and recapture data. We modelled capture probability with an interaction between species and year, a constraint indicated by the previous analysis (see below). We examined effects of species, sex, neckband, and year on apparent survival probability, and effects of sex, species, and year on ψ^{nl}. We selected among 55 competing models using the information theoretic approach described above.

We were able to estimate neckband loss because we recaptured marked geese. In capture-resight studies, neckband loss would be considered mortality (Pollock *et al.*, 1990), and would therefore negatively bias estimates of survival probability. We estimated survival probability ($S^{n\star}$) expected from such capture-resight studies (which include negative bias caused by neckband loss and neckband effects on survival) as: $(S^{n\star}) = S^n \cdot (1 - \psi^{nl})$. Var$(S^{n\star})$ was calculated following Goodman (1960).

6 Neckband effects on true survival and fidelity probabilities

From 46 candidate models including the general model, the best model based on QAIC$_c$ included (1) marker effects on r and a difference between direct (hunting season immediately following the year of marking) and indirect r for legbanded but not neckbanded geese; (2) interaction of species and year effects on p; (3) interaction of species and year effects on F; and (4) interaction of species, marker, and year on S (Table 2). The sum of w_{QAIC_c} for 23 models that included neckband effects on S was 0.99997. Of seven models with $\Delta QAIC_c < 4.0$ (Table 2), all had identical sources of variation on p, and all included multiplicative effects of species, marker, and year on S, except one which did not include species differences in S. Four of these six models included differences between direct and indirect recovery rates for legbanded birds, neckbanded birds, or both groups of birds. Two of these models included effect of neckbands, in addition to species and year, on F. However, the sum of w_{QAIC_c} for 21 models that included a marker effect on F was only 0.213.

Estimates of p_t from the best model ranged from 0.073 ($\hat{SE} = 0.026$) to 0.159 ($\hat{SE} = 0.017$) for white-fronted geese and from 0.028 ($\hat{SE} = 0.006$) to 0.185

TABLE 2. Model structure, deviance, ΔQAIC$_c$, model weight (w_{QAIC_c}), and number of parameters (K) for Burnham (1993) models used; to estimated were effects of species (sp), sex (s), marker (m), and year (t) on capture (p), reporting (r), fidelity (F), and true survival (S) probability of moulting adult white-fronted and Canada geese marked in the Queen Maud Gulf Bird Sanctuary, NU, 1991-1997. Only shown are best approximating models (ΔQAIC$_c$< 4.0) and the most general model from a candidate set of 46 models (variance inflation factor, $\hat{c} = 1.236$). Asterisks denote multiplicative interactions among specified effects.

Model	Deviance	ΔQAIC$_c$	ω_{QAIC_c}	K
$p_{sp \star t} r_m{}^a F_{sp \star t} S_{sp \star m \star t}$	1100.465	0.00	0.356	53
$p_{sp \star t} r_m{}^b F_{sp \star t} S_{sp \star m \star t}$	1100.092	1.71	0.151	54
$p_{sp \star t} r_m{}^c F_{sp \star t} S_{sp \star m \star t}$	1105.073	1.72	0.151	52
$p_{sp \star t} r_m{}^c F_{sp \star m \star t} S_{sp \star m \star t}$	1077.196	3.31	0.068	64
$p_{sp \star t} r_m{}^a F_{sp \star m \star t} S_{sp \star m \star t}$	1074.720	3.32	0.068	65
$p_{sp \star t} r_m{}^a F_{sp \star t} S_{m \star t}$	1139.360	3.33	0.067	39
$p_{sp \star t} r_m{}^d F_{sp \star t} S_{sp \star m \star t}$	1105.053	3.71	0.056	53
Global model	996.21	122.17	0.000	156

[a] r modelled with separate probabilities for direct and indirect recoveries of legbanded, but not neckbanded geese.

[b] r modelled with separate probabilities for direct and indirect recoveries of legbanded and neckbanded geese.

[c] r modelled with time dependency in recoveries of legbanded and neckbanded geese.

[d] r modelled with separate probabilities for direct and indirect recoveries of neckbanded, but not legbanded geese.

($\hat{\text{SE}} = 0.025$) for Canada geese. Direct reporting probability, r^d, was 0.182 ($\hat{\text{SE}} = 0.047$) and indirect reporting probability, r^i, was 0.145 ($\hat{\text{SE}} = 0.025$) for legbanded geese. Reporting probability, r, was 0.129 ($\hat{\text{SE}} = 0.010$) for neckbanded geese.

Under the best model, survival probability varied by species, marker, and year (Table 3). Legbanded geese had higher survival probability than neckbanded geese in every year of the study for both species. Differences in survival probability of white-fronted geese initially marked only with legbands ranged from 0.063 ($\hat{\text{SE}} = 0.083$) to 0.22 ($\hat{\text{SE}} = 0.061$) higher than for those initially marked with

TABLE 3. True survival probability ($S \pm 1\hat{\text{SE}}$) and fidelity probability ($F \pm 1\hat{\text{SE}}$) to the study area of neckbanded and legbanded white-fronted and Canada geese from the Queen Maud Gulf Bird Sanctuary, Nunavut, 1992-97. Parameter estimates are from the best model (Table 2).

		S			F	
	White-fronted geese		Canada geese			
	Legbands only	With neckbands	Legbands only	With neckbands	White-fronted geese	Canada geese
91-92	1.00 ± 0.00	0.78 ± 0.06	0.91 ± 0.05	0.67 ± 0.09	0.61 ± 0.12	0.45 ± 0.07
92-93	0.86 ± 0.04	0.75 ± 0.04	0.92 ± 0.03	0.82 ± 0.04	0.74 ± 0.07	0.82 ± 0.09
93-94	0.91 ± 0.03	0.77 ± 0.03	0.92 ± 0.03	0.77 ± 0.04	0.86 ± 0.08	0.91 ± 0.13
94-95	0.86 ± 0.04	0.71 ± 0.03	0.90 ± 0.03	0.76 ± 0.05	0.60 ± 0.07	0.58 ± 0.11
95-96	0.85 ± 0.04	0.66 ± 0.04	0.86 ± 0.04	0.80 ± 0.05	0.76 ± 0.09	1.00 ± 0.00
96-97	0.81 ± 0.05	0.62 ± 0.05	0.88 ± 0.04	0.82 ± 0.05	0.10 ± 0.01[a]	0.04 ± 0.01[a]
97-98	0.78 ± 0.06	0.72 ± 0.06	0.88 ± 0.04	0.87 ± 0.04	—[b]	—[b]

[a] Product of F and capture probability.
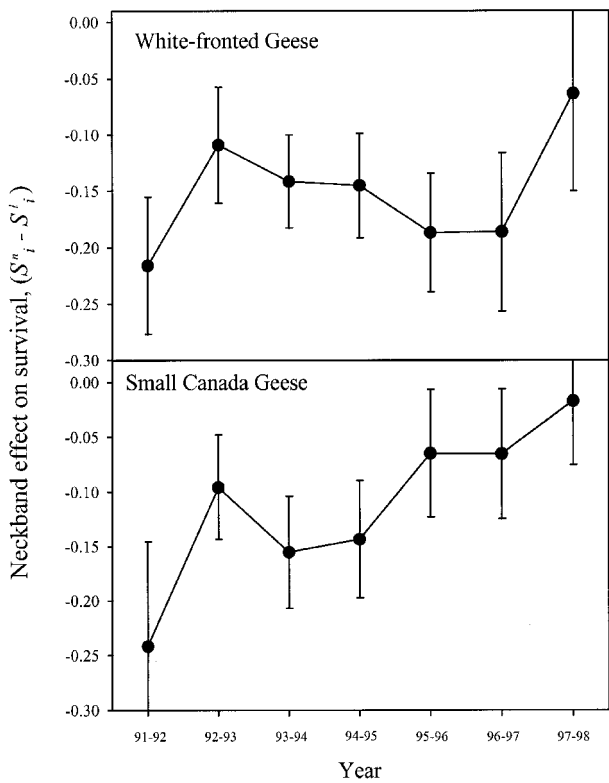
[b] No estimate available.

FIG. 1. Negative effects (± 1 $\hat{SE}$) of neckbands on true survival probability (multiplicative effect) of white-fronted and Canada geese and apparent survival probability (additive effect) of male and female white-fronted and Canada geese banded at the Queen Maud Gulf Bird Sanctuary, NU, 1991-97.

neckbands (Fig. 1). Respective differences in survival probability for Canada geese ranged from 0.017 ($\hat{SE} = 0.058$) to 0.24 ($\hat{SE} = 0.0956$) (Fig. 1). There appeared to be some attenuation of neckband effect on survival probability as the study proceeded, particularly in Canada geese (Fig. 1).

Fidelity probability varied by species and year in all the best models (Table 2) and the multiplicative interaction between species and year effects indicated a lack of consistent species-specific differences. The three best models did not include an effect of neckbands on fidelity probability. However, yearly changes in the probability of fidelity were similar between species (Table 3). Fidelity probability was diminished in 1992 and 1995, but otherwise > 0.70 and highest for both species in 1994 ($\hat{F} > 0.88$). Estimates of fidelity probability in 1997 were confounded with capture probability and therefore available only as a product (Table 3).

7 Neckband loss and apparent survival probabilities

Selection of the best of 54 candidate models during analysis of neckband loss (ψ^{nl}) was unequivocal, with $\Delta QAIC_c = 19.3$ for the second best model. The best model ($w_{QAIC_c} = 0.99994$) included (1) additive effects of species, sex, neckbands, and year on ϕ (Fig. 3) and (2) multiplicative effects of species, sex, and year on probability of neckband loss, ψ^{nl}, including species- and sex-specific trends in ψ^{nl}

with year (Table 4). A model identical to the second best model, except that ψ^{nl} was parameterized in relation to neckband age instead of year, had $\Delta QAIC_c = 62.4$.

To model additive effects of factors on ϕ_t we used a logit link; therefore linearity was not maintained following back-transformation, and thus effect size varied among years. For example, ϕ_t^l was between 0.11 ($\hat{SE} = 0.066$) and 0.07 ($\hat{SE} = 0.066$) higher than ϕ_t^n, and $\phi_t^{'}$ of white-fronted geese was 0.030 ($\hat{SE} = 0.061$) to 0.047 ($\hat{SE} = 0.066$) higher than ϕ_t of Canada geese. Finally, $\phi_t^{'}$ of female geese was 0.019 ($\hat{SE} = 0.060$) to 0.030 ($\hat{SE} = 0.067$) higher than $\phi_t^{'}$ of male geese.

From the best model, slopes in logit scale of temporal trend in neckband loss, ψ^{nl}, with year was negative for Canada geese (for females, $\beta_1 = -0.812 \pm 0.362$ ($\hat{SE}$); for males, $\beta_1 = -0.579 \pm 0.212$) and positive for white-fronted geese (for females, $\beta_1 = 0.438 \pm 0.178$; for males, $\beta_1 = 0.856 \pm 0.144$). Rate of neckband loss exceeded 0.4 for males of both species in some years, but the highest probability of loss for females was 0.158 ± 0.074 (Table 4). The product of sex-, and species-specific rates of neckband loss, and respective annual survival probability of neckbanded birds gives the predicted survival probability ($S^{n\star}$) if neckbanded geese in this study are reobserved during migration or winter, as is normally done in a capture-resight study. This estimate ranged from 0.38 to 0.87 (Table 4).

8 Discussion

Neckbands reduced the survival probability of white-fronted and Canada geese banded in the Queen Maud Gulf Bird Sanctuary. Our findings are consistent with Samuel *et al.*'s (1990a) observations of reduced survival probability for neckbanded, juvenile Canada geese in Wisconsin and Castelli & Trost's (1996) finding of the negative effect of neckbands on the survival probability of Canada geese from New Jersey. Menu *et al.* (2000) suggested that Castelli & Trost's (1996) results may have been biased because they failed to consider models with both direct and indirect recovery rates. Our study indicates that the magnitude of neckband effects on survival probability varied little between models with and without constraints on direct and indirect recovery rates. Our results are also consistent with the findings of Schmutz & Morse (2000), who concluded that emperor geese (*Chen canagica*) marked with tarsal tags had higher survival probability than emperor geese marked with three different types of neckbands. Our conclusions differ from Menu *et al.*'s (2000) finding of similar survival probability for neckbanded and legbanded greater snow geese (*Chen caerulescens atlantica*) and Samuel *et al.*'s (1990a) findings for adult Canada geese. We suggest that our conclusions carry higher inferential strength than other studies about effects of neckbands on survival to date because of our higher sample size.

We found no unequivocal evidence that probability of permanent emigration was higher for neckbanded compared to legbanded geese. Schmutz & Morse (2000) and Menu *et al.* (2000) speculated that neckbands may reduce breeding probability (temporary emigration) of geese, because their summer detection probabilities (estimated with CJS models) were lower for neckbanded than leg-banded geese. However, breeding probability in these analyses was confounded with detection probability, given presence on the study area (see also MacInnes & Dunn, 1988). Specific methods (Lindberg *et al.*, in press) are required to address questions about effects of neckbands on permanent or temporary emigration.

Samuel *et al.* (1990a) concluded that true survival probability of neckbanded, juvenile Canada geese was 0.099 lower than legbanded juveniles. Castelli & Trost

TABLE 4. Annual rates of collar loss (ψ^{nl}) for male and female white-fronted and Canada geese double marked with neckbands and legbands at Queen Maud Gulf Bird Sanctuary, Nunavut, 1991–1999. Estimates of ψ^{nl} are from the best model. Also shown are estimated survival probabilities (e.g. $S^{n\star}_{male} = [1 - \psi^{nl}_{male}] \star S^{n}$) predicted for neckbanded geese as though from a mark-resight study during migration or winter using Cormack-Jolly-Seber (CJS) models; estimates of S^{n} are from Table 3.

	White-fronted geese				Canada geese			
	ψ^{nl}_{female}	ψ^{nl}_{male}	$S^{n\star}_{female}$	$S^{n\star}_{male}$	ψ^{nl}_{female}	ψ^{nl}_{male}	$S^{n\star}_{female}$	$S^{n\star}_{male}$
1991-92	0.005 ± 0.002	0.002 ± 0.002	0.78 ± 0.06	0.78 ± 0.06	0.158 ± 0.074	0.434 ± 0.095	0.57 ± 0.09	0.38 ± 0.08
1992-93	0.007 ± 0.005	0.005 ± 0.003	0.75 ± 0.04	0.74 ± 0.04	0.077 ± 0.022	0.300 ± 0.047	0.76 ± 0.04	0.58 ± 0.05
1993-94	0.011 ± 0.006	0.011 ± 0.005	0.76 ± 0.03	0.76 ± 0.03	0.036 ± 0.013	0.194 ± 0.031	0.74 ± 0.04	0.62 ± 0.04
1994-95	0.017 ± 0.006	0.026 ± 0.008	0.71 ± 0.03	0.71 ± 0.03	0.016 ± 0.011	0.119 ± 0.036	0.74 ± 0.05	0.67 ± 0.05
1995-96	0.026 ± 0.007	0.058 ± 0.012	0.65 ± 0.04	0.63 ± 0.04	0.007 ± 0.007	0.070 ± 0.035	0.79 ± 0.05	0.74 ± 0.05
1996-97	0.040 ± 0.011	0.127 ± 0.018	0.60 ± 0.05	0.54 ± 0.05	0.003 ± 0.004	0.041 ± 0.029	0.81 ± 0.05	0.79 ± 0.05
1997-98	0.060 ± 0.022	0.255 ± 0.043	0.68 ± 0.06	0.654 ± 0.06	0.001 ± 0.003	0.023 ± 0.022	0.87 ± 0.05	0.85 ± 0.05
1998-99	0.090 ± 0.044	0.446 ± 0.085	—[a]	—	0.001 ± 0.001	0.013 ± 0.015	—	—

[a] Not calculated because estimate for S_{98-99} unavailable (Table 4).

(1996) found a similar reduction (0.135) in true survival probability of neckbanded Canada geese in New Jersey, and Schmutz & Morse (2000) estimated that apparent survival probability of neckbanded emperor geese was 0.167 lower than survival probability of emperor geese marked with tarsal bands. An exception to these findings was that Menu *et al.* (2000) reported that true survival probability of greater snow geese with neckbands was 0.034 higher than for geese without neckbands, and that apparent survival probability of the two groups of geese was equal.

Like Menu *et al.* (2000) we used several types of analyses to estimate the magnitude of differences in population parameters for neckbanded geese compared to those without neckbands. We estimated that true survival probability was 0.24 ($\hat{SE} = 0.096$) to 0.017 ($\hat{SE} = 0.058$) lower for neckbanded geese than for those without neckbands using Burnham's (1993) model, and that this effect was similar among sexes within a species (Tables 2, 3). However, we suspect that neckband loss may have led to underestimation of neckband effect size on true survival. Geese assigned to the experimental group effectively entered the control group if they lost a neckband, and this was beyond our control when using Burnham's model. We found little evidence that fidelity probability was affected by neckbands in this same analysis, although differences in fidelity may have been similarly confounded somewhat by neckband loss. However, controlling for neckband loss in our multistate analysis, we found that neckband effect on apparent survival, i.e. the product of true survival and fidelity probability, in the best model remained constant over time (Fig. 3). Moreover, temporal variation in apparent survival probability from that analysis (Fig. 3) paralleled temporal variation in fidelity probability estimated from Burnham's model (Fig. 2). Assuming lack of a neckband effect on fidelity from Burnham's model, estimates in apparent survival from our multistate analysis suggested that differences between treatment and control groups were due to differences in true survival, differences that were constant over time. This finding, considered together with estimation of neckband effect on true survival using Burnham's model, is consistent with the notion that neckband loss accounted for apparent attenuation in neckband effect on true survival as the study progressed (Fig. 1).
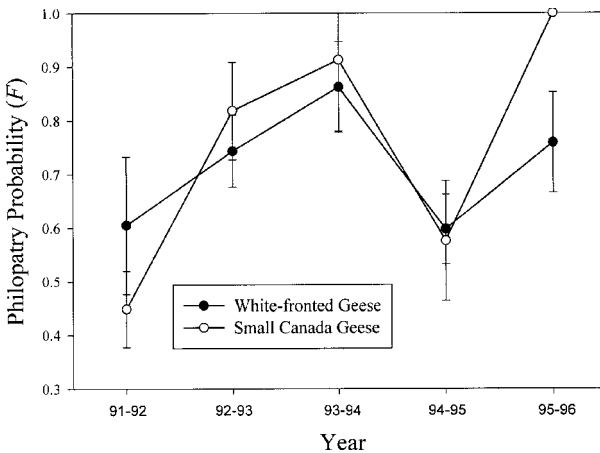

FIG. 2. Fidelity probability ($F \pm 1 \hat{SE}$) of moulting white-fronted and Canada geese to the Queen Maud Gulf Bird Sanctuary, Nunavut, 1991-96.
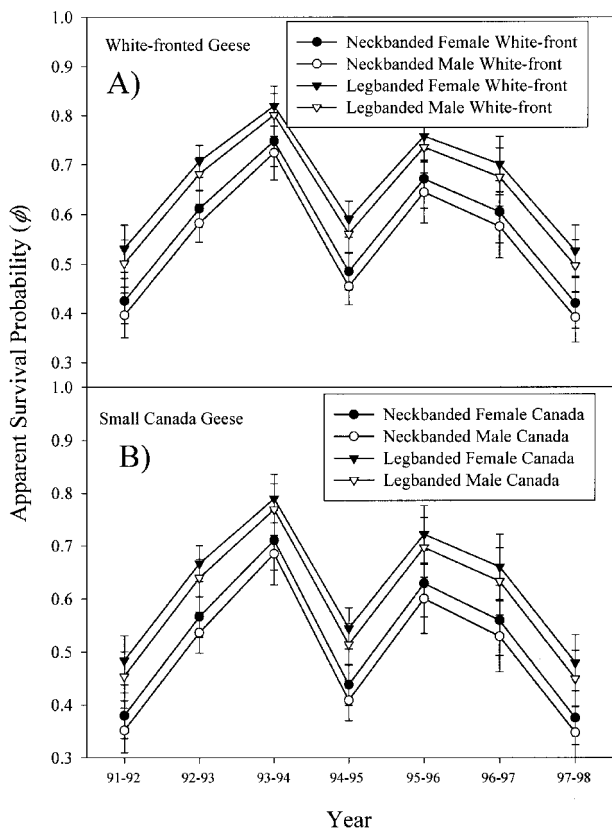
FIG. 3. Additive relationship between the effects of sex, species, and marker type (legband or neckband) on apparent survival probability (± 1 ŜE) of white-fronted and Canada geese moulting at the Queen Maud Gulf Bird Sanctuary, NU, 1991-98.

Like past studies, we did not identify causes of the observed neckband effect. Three mechanisms for how neckbands may reduce survival probability have been proposed: (1) icing of neckbands (e.g. MacInnes *et al.*, 1969; Craven, 1979; Zicus *et al.*, 1983); (2) hunters selecting neckbanded geese (e.g. Samuel *et al.*, 1990a, Castelli & Trost, 1996), and (3) nutritional/energetic/thermoregulatory costs (e.g. Ankney, 1975; Schmutz & Morse, 2000) increasing non-hunting mortality. We suspect that both icing and energetic/thermoregulatory costs could impinge upon survival probability of geese in this study because these geese occur in arctic habitats and migrate long distances between moulting and wintering areas. From locations of legbands recoveries reported by hunters, the Small Canada geese in our study winter largely in SE Colorado and the Texas panhandle, whereas most midcontinent white-fronted geese winter near the Gulf of Mexico Coast in Texas and Louisiana, and increasingly in Arkansas. From unsolicited reports, 13 Canada geese but no white-fronted geese marked with neckbands by us were documented to have encountered neckband icing (K. Meeres, personal communication). This is consistent with the higher winter latitudes of small Canada geese compared with white-fronted geese. However, it is also consistent with the greater surface to volume ratio (likely with greater potential for capillary action for water when on roost ponds, and consequently higher likelihood of icing) of double wrap neckbands

used on Canada geese compared with those on white-fronted geese (see also MacInnes *et al.*, 1969). Nevertheless, the magnitude of the bias was similar between species regardless of neckband design or winter latitude. Unfortunately, any effect of neckband design on survival probability was confounded with independent biological effects specific to each species, because our choice of neckbands had to be consistent with the marking protocol of the larger effort to mark and resight neckbanded geese from across arctic Canada and Alaska.

Our analyses include the first use of multistate models to estimate loss probability for neckbands. We think this is a tractable approach to model tag loss particularly when parameters may differ between individuals marked with different types of markers and individuals move from experimental to control groups following marker loss. Other studies have relied on hunter questionnaires (Samuel *et al.*, 1990b; Hines *et al.*, 1999), which may suffer from, for example, non-response bias (see also Nichols & Hines, 1993).

Effects of species and neckband type on loss rates were confounded in this study, because white-fronted geese and Canada geese were marked with different types of neckbands (see above). We were surprised by the lack of evidence to support neckband age as a factor in our analysis given frequent support of this factor in past studies (e.g. Nichols & Hines, 1993; Johnson *et al.*, 1995). We were equally surprised by the opposite trends in loss probabilities for the species/neckband types. These results must have been unrelated to any temporal variation in our methodology during marking, which was consistent for both species over the course of the study. Alternatively, temporal trends in environmental conditions may have influenced loss probability. We do not fully understand how these conditions could have differed for the two species or respective neckband types, but we offer suggestions. For example, hunting pressure may affect loss rate. Geese were often recaptured with neckbands damaged by shot (RTA, personal observation), although this was not noted for each recapture. Information specific to small Canada geese is not available, but numbers of midcontinent white-fronted geese killed and retrieved by hunters in Alberta, Saskatchewan, and the Central and Mississippi Flyways, where virtually all midcontinent white-fronted geese are shot, has increased by an average of 28% annually from 1990-1999 (Fig. 4). Such increases in harvest pressure may have accounted for increasing rates of neckband loss in that species. We did not include harvest as a covariate in our modelling because the most appropriate annual covariate is harvest rate, which we do not know. Nevertheless, increasing harvest rate may provide a plausible explanation for increased damage to existing neckbands on geese that encounter shot but survive a hunting season.

We also observed sex-specific differences in loss probabilities for both species, with males losing neckbands at a higher rate than females. Higher neckband loss rates for male than female geese and swans has been reported by others (Fjetland, 1973; Samuel *et al.*, 1990b; Nichols *et al.*, 1992; Johnson *et al.*, 1995; Hines *et al.*, 1999; Wiebe *et al.*, 2000). Part of the explanation may lie in the more aggressive nature of males compared to females during winter (e.g. Raveling, 1970), or perhaps during courtship or territorial behaviour on breeding areas (Johnson *et al.*, 1995), which may cause neckbands already damaged by shot or other causes to fall off.

Another potential source of bias that we did not quantify was diminished visibility of codes on neckbands as they age. Inability to read codes even if the neckband is detected during observations outside the marking period would render those
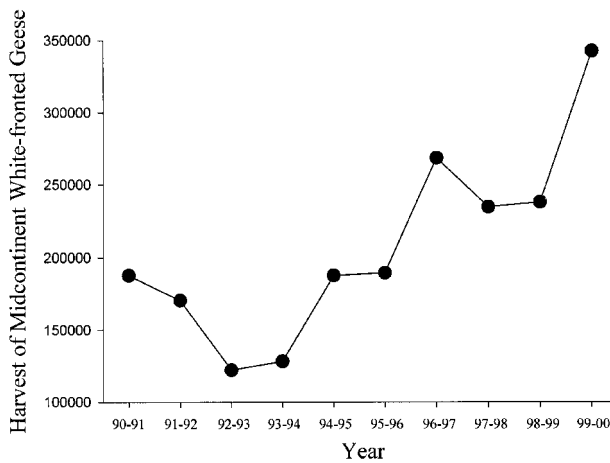
FIG. 4. Harvest of midcontinent white-fronted geese in Alberta, Saskatchewan, Central and Mississippi Flyways, during hunting seasons of 1991-1992 to 1999-2000 (from Martin & Padding, 2000).

neckbands effectively lost to observation, further amplifying bias associated with neckband loss. This reinforces our general conclusion with regard to loss rates: because of the high loss rates for both species/neckband type combinations, researchers should be extremely cautious about the use of these neckband types for these species.

9 Research and management implications

Reduced survival probability directly caused by neckband presence can have important implications for management decisions. When information on recruitment is available, then estimates of survival probability can be used to calculate rates of population change (λ) as $\lambda = R + S$, where R and S denote recruitment and adult survival, respectively. For example, if we assume a stable population with $\lambda = 1$, then $R = 0.13$ (the product of clutch size, breeding propensity, and survival of nests, goslings, juveniles and pre-reproductive adults), given that $S^l = 0.87$ (unweighted mean annual survival for white-fronted geese without neckbands in this study). If, however, $S^n = 0.72$ (unweighted mean annual survival for white-fronted geese with neckbands in this study, see Table 4), then $\lambda \approx 0.83$ leading to the incorrect inference of a substantial population decline of $\approx 17\%$ per year. Use of survival estimates biased by neckbands might have led to the conclusion that, by 1998, white-fronted goose populations would have declined within our study area to only 32% of levels at the start of our study in 1991. Use of $S^{n\star} = 0.70$, the unweighted mean survival rate expected from a mark-resight study (i.e. negatively biased by neckband effects on survival probability and neckband loss), might have led to the conclusion that population levels had declined to only 27% of initial population size. The magnitude of the effect that biased estimates of survival probability (through a direct effect of neckbands on survival, further compounded by neckband loss) can have on population projections could motivate misguided management action.

Hestbeck *et al.* (1990) reviewed trade-offs between sample size of marked geese, re-encounter rates, and precision in estimates of survival probability. At the time

of their review, recovery rates of geese from Brownie *et al.*'s (1985) models of band recoveries from birds shot by hunters were comparatively low (see also Shaeffer & Malecki, 1995). Hestbeck *et al.* (1990) argued that, because of higher resighting rates possible with reobservation studies of live geese, compared with recovery rates from hunter-shot birds, CJS models should provide estimates of survival with greater precision than Brownie *et al.*'s models. Fewer geese need to be marked with neckbands than with legbands to achieve similar precision in estimation of survival probability, when band returns are not solicited. Hestbeck *et al.* (1990) were careful to review possible problems of neckbands, but suggested that, depending on the needs of the study, neckband studies of geese could be superior to legband studies due to increased precision in estimation, and reduced cost. Our findings make us question if increased precision is outweighed by increased bias.

Foremost, we strongly urge researchers to test assumptions about marker effects on population parameters of interest. Such evaluations are possible when done as part of regular banding operations where treatment and control animals are recaptured and survival is estimated from recoveries of dead birds (Burnham, 1993). However, marker effects may lead to flawed inferences about movement and associated transition probabilities. For example, if markers influence the condition of birds, then diminished condition may result in greater likelihood of movement among, say, winter areas. Our results suggest that the product of probabilities for site fidelity and non-breeding was not influenced by marker effects, but we were unable to assess marker effects on each probability separately because we did not mark breeding birds in the same area.

We advocate recapture of doubly marked animals not only for studies of geese, but for most wildlife on which markers are used, particularly in situations for which there may be even anecdotal or circumstantial evidence suggesting a marker loss or an effect on survival. In the best case, biases are absent (Menu *et al.*, 2000). The next best situation involves the ability to correct for the bias, even if one exists (see Nichols *et al.*, 1992). For example, estimates of population parameters from marked animals may be calibrated to the control sample without marks, such as when the marker effect is additive to annual variation in the parameter of interest, i.e. when the effect size of markers on the parameter is more or less constant among years. The most problematic situation is when degree of marker bias varies with another source of variation, e.g. when effect size of markers and loss rates vary among years (i.e. as found in this study, possibly due to increasing harvest rate on at least white-fronted geese). In such situations, calibrating parameter estimates from the marked population must be done for each year with a cost of reduced precision (Pollock, 1981). Otherwise, use of markers may yield highly biased estimates, and use of these estimates in population models will result in incorrect inferences.

Neckband studies of geese can still be useful in experimental manipulations with treatment and control groups to evaluate treatment effects on vital rates (e.g. Samuel *et al.*, 1999). In such cases, the researcher should (1) be willing to accept some loss of animals, and (2) estimate loss rates of neckbands for proper inference.

Acknowledgements

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